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THE ORIGIN AND FORMATION OF THE FROTH IN SPITTLE-INSECTS[1]

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During the summer months one observes upon trees, shrubs, herbs and grasses, numerous masses of froth-like material, which resemble large drops of spittle. An examination of a frothy mass soon discloses the presence of a small insect, greenish, brownish, or whitish in color, depending upon the species under observation. This is the immature nymphal stage of an insect belonging to the homopterous family Cercopidæ. So far as it is known, all the members of this family surround themselves with such a secretion, in which they spend their nymphal life. I have had under observation three species, *Aphrophora parallela* Say, *Lepyronia quadrangularis* Say, and *Clastoptera proteus* Fitch. Each of the species studied in this locality makes a characteristic froth, as may be easily recognized by a little study.

While there is much which has been written upon the production of froth by the insects of this group, the opinions of the many writers are very much at variance. This is especially true regarding the more recent literature on the subject. For this reason it seemed desirable to undertake a detailed study of this subject and to determine what organ or organs were concerned in the production of this secretion. This study consisted not only of field observations and laboratory experiments, but of a detailed study of the histological structures concerned.

This work was carried on in the Entomological Laboratory of Cornell University, and to its director, Professor J. H. Comstock, I am indebted for many courtesies. The problem was suggested by Dr. W. A. Riley, and to him I am indebted for constant aid and advice.

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[1] Contribution from the Entomological Laboratory of Cornell University.

HISTORICAL

Gruner (1901) has given a very extended and excellent historical account of the work of individual writers on these insects. It is intended here merely to group the views held by the various writers, at the same time adding the opinions held by writers since the appearance of Gruner's paper.

As far as the writer has been able to determine from original sources, there are seven theories which have been advanced in explanation of the production of the froth. This does not take into account the belief of the southern negroes, who claim that the frothy masses are caused by horseflies, neither does it take into consideration the opinion formerly held by many, that it is the product of the stars, nor the view that it exudes from the ground.

Isidorus, who lived in the sixth century, is cited by Gruner as the first to write on this subject. He believed that the froth was the spittle of the cuckoo bird, and that from this secretion the cercopid spontaneously generated. Mouffet (1634) and other writers came to the same conclusion respecting the origin of the spittle and insect. Aldrovandi (1610), in his Ornithologia, strongly denies this assertion, but fails to enlighten the reader as to the true solution of the problem.

According to Gruner's account, Bock (1546) apparently believed that the froth was the product of plants and he gave a list of the plants producing it.

John Ray (1710) states that the spittle mass was caused by the insect found within the mass, and believed that it was expelled from the animal's beak. He was upheld in this view even in recent times by as prominent an authority as Uhler (1884). Fabre (1900) states that a clear fluid comes out of the beak and that to this fluid the insect injects air bubbles by grasping air with the last pair of lateral prolongations of the ninth abdominal segments.

Blankaart (1688) believed that the froth came out of the anal opening of the insect. In this view he is supported by Poupart (1705), Frisch (1720), Geoffroy (1764), DeGeer (1773) and others. Morse (1900) modified this view somewhat in that he gives as his opinion that what comes out of the anus is a " clear somewhat viscid fluid " and that by means of appendages at the extreme tip of its abdomen the insect secured a moiety of air by grasping it, so to speak, and then instantly releasing it as a bubble into the fluid. Gruner (1900 and 1901) states that the fluid is exuded from the anus and passes under the body, flowing into a pocket-like space where it becomes impregnated with air which comes out of the stigmata located in the pocket.

Porta (1900 and 1901) believed that there were openings on the dorsum of Aphrophora which were connected with oval glands little distinct from the hypodermis. He describes them as arranged at the base of the excretory canal in numbers of five, six or even fewer, indistinctly separated from one another. To these glands he ascribed the function of producing the fluid. He also states that the bubbles are blown into the fluid by the method described by Morse.

Girault (1904) states that " during the process of secretion the fluid flows slowly from a point near the anal opening, and gathers between the legs, where, by their alternate agitation, it becomes mechanically mixed with air and forms cushions of air bubbles," and he further states "that the air is taken in at each up and down motion of the abdomen and that during this dipping process the ventral plates are in transverse motion like jaws, and that it is probable that the secretory glands are between them." From this we should infer that he thought that it came from special secretory glands and not from the anus.

Berlese (1907) believes that the froth is secreted by glands found upon the seventh and eighth abdominal segments, previously described by Batelli (1891).

In the following it is proposed to discuss the evidences bearing upon each of the current views presented above and give in details the observations made to clear up the confusion.

METHODS

The methods used in the biological observations are given in the body of the text. I refer here only to those used for the examination of the histological structures.

In preparing the tissues of the spittle insects for histological examination various methods of fixing, killing and staining were used. The best results were obtained by killing in hot water and then transferring immediately into Fleming's strong solution for twenty-four hours. Tissues killed directly in hot Fleming's fluid, while giving satisfactory differentiation of organs like the testes, intestine and fat cells, gave poor results with the glands. Very good results were obtained by killing in hot Gilson's fluid.

Good serial sections of the nymphs were obtained by infiltrating in paraffine 54° C., while adults imbedded in 62° C. paraffine gave better sections. Sections were cut from three to ten microns.

Staining was done on the slide with iron hæmatoxylin or Delafield's. Whenever the latter was used the tissues were counter-stained in eosin.

In order to get satisfactory preparations of the glands in surface view the tissues were killed in hot Gilson's fluid and allowed to stand for one half hour after having been opened and the fat carefully removed. After washing in seventy per cent. alcohol and a few drops tincture of iodine, the specimens were stained in borax carmine for a few minutes, dehydrated, cleared and mounted in balsam. Great care must be observed in teasing the fat away from the glandular region, otherwise the cells will be disarranged.

PERSONAL OBSERVATIONS UPON THE PRODUCTION OF THE FROTH

I first studied the gross features of the froth formation in several specimens. A large specimen of *Aphrophora* *parallela* was taken from the frothy mass and by means of a camel's hair brush was thoroughly freed from every particle of froth. The specimen was then placed upon a dry twig. It soon inserted its beak in the plant and gradually increased in size. It projected the tip of its abdomen extensively and then retracted it. This operation it repeated several times. Suddenly a small drop of a clear liquid appeared at the very tip of the abdomen, coming distinctly out of the anal opening. Observations made with a hand lens upon other parts of the body, especially in the region of the dorsum, failed to show any fluid whatever. The small drop was soon joined by another, and these in turn were followed by many others, the whole mass of fluid passing down on the ventral side of the body along the channel formed by the sternites and the prolongations of the pleurites (Figs. 1 and 6). Again, the fluid was noticed to be fairly oozing out of the anal opening. After a quantity had accumulated about the body of the insect, it was noticed that the last pair of legs, sometimes also the second pair, would reach out to the region of the seventh and eighth abdominal segments, then rub against the body and against one another as if in the process of mixing substances. After the fluid had been well mixed and the surface had been covered by it, it was next observed that the nymph moved the tip of the abdomen out of the liquid, opening up the pair of lateral appendages of the ninth abdominal somite, which immediately closed again. Then with a downward movement these parts were immersed in the liquid and the appendages, upon being opened, released a particle of air in the fluid. This operation was repeated many times, with the result that the insect was soon covered with air bubbles, which gave the characteristic covering a froth-like appearance. It was noticed that by changing the size of the air-grasping pocket, the insect is able to make bubbles of any size. For that reason, the bubbles in the smaller forms are always very much smaller than those of the larger spittle insects. It is partly this feature which determines the above-noted characteristic appearance of the froth of the different species. The insect does not always wait until the body is completely covered with fluid before injecting the air into it.

In order to make sure that the larger portion of the fluid came only from the anus, the latter was closed by a plug of lens paper, which being capped with balsam, and then allowed to dry for a few moments, closed the anal opening perfectly. The insect, upon being placed on a twig, after locating a satisfactory place, soon pierced the plant with its beak and began feeding. It rapidly increased in size and became much distended and swollen. Although observed for over three hours not a single drop of fluid came out. In a specimen whose anal opening had not been carefully sealed a drop of liquid succeeded in coming out of the tip of the abdomen, on the side of the filter plug. Thus it was demonstrated, as any one who desires to repeat the operation may, that at least one of the constituents of the froth is emitted from the anal opening, and that the views of Mouffet, Porta, Berlese and Girault are not correct, for according to their interpretations the closing of the anus would not interfere with the production of the froth.

Histological Study of the Structures of the Glands of Batelli

While it is seen that the greater portion of the liquid from which the froth is produced is derived from the anus, there arises the question whether there are not other organs, the secretion of which may take a prominent part in the formation of the spittle.

In the pleural region of the seventh and eighth abdominal somites very large hypodermal glands are located. To the naked eye these glands are not easily discernible upon the nymph, their positions being detected only if there happens to be a large supply of their secretion. Under the hand lens when the abdomen is extended, there are to be noticed whitish patches, even when the secretion has been completely removed. These, which lie in about the mid-pleural region, are somewhat pulvinate in shape, but by no means regular in outline.

As to the location of these glands there seems to be some difference of opinion. Batelli (1901) describes them as being located on the last two abdominal segments. Misinterpreting Wheeler's (1889) account of the adenopodia of the first abdominal segment in embryos of Nepa and Cicada, he erroneously homologizes these glands of Aphrophora with such structures, but rejects Wheeler's view that they are homologous with abdominal appendages. Porta (1900) and Gruner (1901) believed that these glands are situated on the seventh and eighth abdominal segments, while recently Berlese (1907) gave as his opinion that they were located on the eighth and ninth abdominal somites. I am of the opinion that Porta is correct, for there is no evidence that the first abdominal segment has been suppressed and they are clearly on the existing seventh and eighth abdominal somites (Fig. 2). Morever, this would harmonize more fully with Ber-

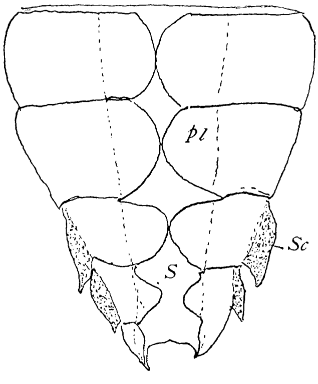

FIG. 1. Ventral View of full-grown Nymph of *L. quadrangularis*, ×40. *Pl*, pleural prolongations; *Sc*, secretion of the glands of Batelli; *g*, groove.

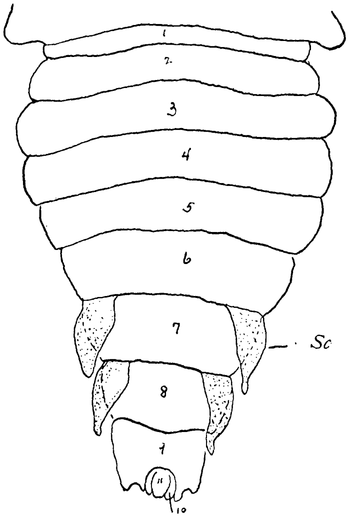

FIG. 2. Dorsal View of younger Nymph of *L. quadrangularis*, ×40. 1-11, tergites; *Sc*, secretion.

lese's own labeling of the segments in the abdomen of *Cicada plebeia* (*Gli Insetti,* Fig. 297, page 263).

An examination of the cuticle in the region of the seventh abdominal gland under the 3 mm. objective of the compound microscope shows that it is free from hairs, which are more or less abundant in other regions of the body. Under the one-sixteenth-inch oil immersion objective one is able to readily discern numerous minute pores (Fig. 3), giving it the appearance of very fine ingrained leather. These pores are more or less regularly distributed over the surface, equally distant from one another, and of equal size throughout the region. Similar pores were found on the eighth abdominal pleura. The most diligent search failed to reveal any such structures in any other region of the body. As I shall emphasize later, these are the openings of true cuticular pores through which the secretions of the underlying glands emerge to the surface.

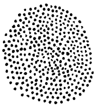

FIG. 3. Surface View of the cuticular Pores overlying the Glands of Batelli.

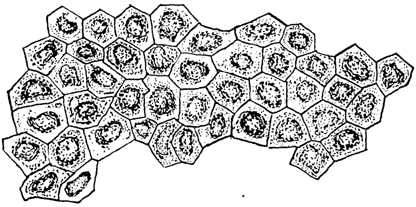

FIG. 4. Surface View of the Epithelium of the Glands of Batelli, x 250.

Specimens of the spittle nymphs were opened and the underlying fat carefully removed. Although it is difficult to separate the fat from this region without destruction of the glands, enough was removed so as to present a satisfactory area for study. The cells (Fig. 4) in good preparations were clearly defined, mostly hexagonal (occasionally pentagonal), though somewhat irregular from mutual pressure. They lie in close apposition to one another. The nuclei are large, round or oval, and in surface view appear situated in the center of the cell.

They are granular and occupy a large portion of the cell. The protoplasm in the region of the nuclei is highly granular and is readily stained. In the periphery of the cell it is not stained as readily, appearing somewhat hyaline. In some of the preparations made with specimens which had been killed in alcohol there were a number of intercellular spaces, while in the preparation of the glands which had been fixed immediately after removal of the fatty tissues such appearance was lacking, except in places where it was obviously due to mechanical cause. Arnhart (1906) gives a photomicrograph of a surface view of the wax-glands of bees, and explains these openings as tracheal in nature. Their presence is, in my opinion, due solely to faulty preparations rather than to the presence of any special tracheal ramifications. In general appearance the cells in surface view are very similar to those of the wax-glands of the honey-bee. A comparison with the excellent figures of Dreyling (1905) serves to bring this out clearly.

In longitudinal sections of *A. parallela* and *Lepyronia quadrangularis* the hypodermal cells of this region are greatly enlarged (Fig. 5), and strikingly resemble those of the wax-gland of the bees. Each gland has the appearance of a curved band or bow, the central portion of which is thick, while it gradually tapers towards the ends. The same thing is noticed in the cross section (Fig. 6). This appearance is due to the general decrease in height of the

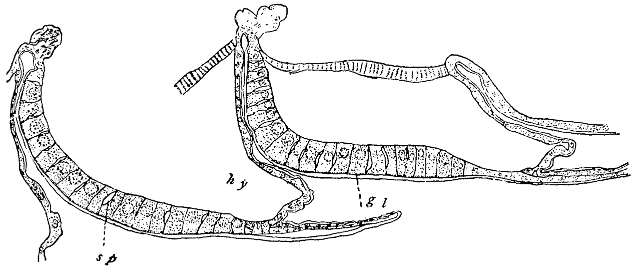

FIG. 5. Frontal Section of the Glands of Batelli in the Nymph of *Lepyronia quadrangularis*, × 125. *Gl*, glandular epithelium; *hy*, ordinary hypodermis of the body-wall; *sp*, spaces.

individual cells from the center to the periphery of the glandular mass. The cells in the main body are sharply defined, being separated from one another by distinct lines of demarcation. Near the margin of the gland it is not so easy, however, to define the contour of the individual cells, these passing gradually into the regular type

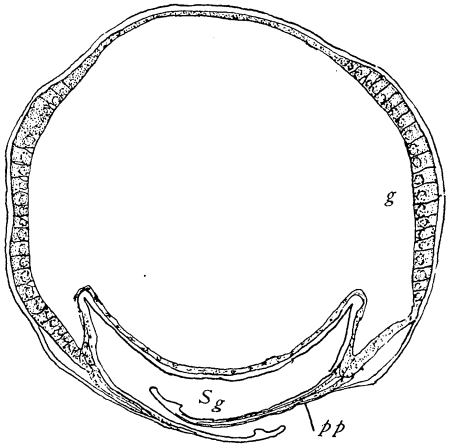

FIG. 6. Cross section of the seventh Abdominal Segment showing the Glands of Batelli, ×110. *Sg,* sternal groove; *pp,* pleural prolongations.

of hypodermal cells. In this type the nuclei are smaller and the cell outlines are not discernible. In sections of the gland the cells are not uniform in width, due to the fact that the sections pass in the center of some and in the sides of others. The glands of the two segments are about equal in size. In sections that pass through the long axis they are 292 microns in *Lepyronia quadrangularis,* and in *A. parallela* they are 465 microns. Most of the sections which the writer has made show clear spaces (*sp.,* Fig. 5) between the individual cells. These spaces vary in their appearance in different preparations, and evidently represent artifacts due to faulty fixation, rather, than the normal appearance of the cells.

In the middle of the glands the cells are high, cylindrical or cubical. On the margin they are low. In the last instar of the nymphs of *A. parallela* they are 30 microns in height and 18 microns in width in the center of the gland, while in the margin the measurements are approximately 16 by 14 microns. The nuclei are round or oval and are situated in the lower margin of the cell. They are very granular and stain deeply. They are about 8 by 6 microns in dimensions. The protoplasm is highly granular, much more so in the region of the nuclei and in the margin underneath the chitin. The cuticula over the gland is about 8 microns thick, while that of the adjacent body wall is 12 microns.

If one makes satisfactory sections through the glands of these insects it is very easy to see extremely minute openings in the overlying cuticula leading from the glands to the surface. These outer openings correspond to those described above. For each canal there is a pore. Their distribution over the gland is regular. They are unbranched, perpendicular to the surface of the cells and about equally distant from one another (Fig. 7). As has been stated, similar pores do not occur in other regions of the body wall. Berlese (1907) and many other writers hold the opinion that true pores are never present in the chitin, and that substances are not conducted through the chitin by any such arrangement. Dreyling (1905), in a paper already referred to, figures and describes canals in the chitin overlying the wax cells of the social bees, and ascribes to these the function of conveying wax to the outer surface. Many writers agree with Dreyling in this view. My studies of the cuticula in the spittle insect convinces me that such true pores are present and they do serve as conduits in carrying the secretions of the underlying glands to the surface. It was noticed on several occasions that in specimens dropped in hot Flem-

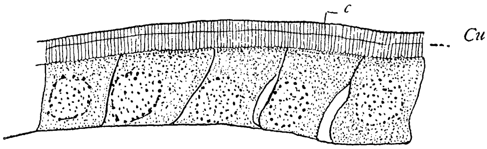

FIG. 7. Enlarged Portion of the Gland of Batelli, showing the cuticular canals, x 275. *Cu,* cuticula ; *c,* canals.

ing's fluid the region of the glands was always immediately darkened, while the other parts were not so affected. This was evidently due to a more rapid penetration of the fluid at the point, or the staining of the secretion within the pores.

The above-described glands are also present in the imago, but in this stage they are very greatly reduced in size (Fig. 8) and show many signs of degeneration. The high cylindrical condition of the cells noted in the nymphal stage is absent, and the sharply defined cell divisions are not present. The protoplasm is scanty and not so granular as in the nymphal stage. Many of the cells show signs of breaking down. Scattered throughout the glandular mass one finds many irregularly shaped bodies which are stained of a pinkish color by the eosin. No spaces were noticed between the individual cells. The nuclei are round and oval and of about the same size noted for the nymph. They show signs of breaking down, in fact some of them are surrounded by clear space, and many had a shrunken appearance.

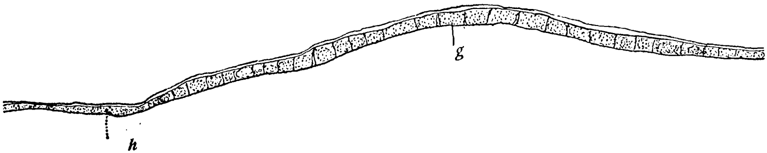

FIG. 8. Gland of Batelli in adult Insect, × 200. *G*, gland; *h*, ordinary hypodermis.

FUNCTION OF THE GLANDS OF BATELLI

Morse (1900) states that "On the sides of the seventh and eighth abdominal segments may be clearly seen leaf-like appendages, which are possibly branchial in nature." These he figures and describes as "extremely tenuous and having the appearance of clusters of filaments, slightly adhering together and forming lamellate appendages similar to the gill-like appendages seen in the early stages of Potamanthus," though he admits they do not have the definiteness of these structures. Specimens he placed in water lived for some time and he concludes that the above-referred to structures have a respiratory function. These so-called branchial tufts of Morse (*sc.,* Figs. 1 and 2) are nothing more nor less than the plates of secretion from the glands described above. This secretion is not filamentous, but appears rather very granular. It is very easy to remove these flakes of wax by means of camel's hair brush from the segments to which they adhere but slightly. The secretion is not soluble in alcohol and swells up after being allowed to stand in water for some time. It has a very striking superficial resemblance to beeswax.

The resemblance of these glands to the wax-glands of the honey bee, in the shape of the cells and in the location and appearance of the nuclei is very striking. This fact has already been pointed out by Batelli (1891), Gruner (1901) and others, who also find much in common with the cells of the wax-glands of coccids and other Hemiptera. Gruner (1901) thought that the *wax* served to line the "pocket" already mentioned so as to enable the air to penetrate it the better, and prevent the inflow of the fluid while the bubbles of air were being blown into the fluid. Porta (1900) accepting Morse's curious error regarding the presence of branchiæ, considered this thickened epithelium as a supporting structure for these supposed gills. Carrying further Batelli's misinterpretation of Wheeler's work, he regarded these "supporting structures" as homologous with the abdominal appendages of the embryos of Nepa and Cicada.

I am convinced that these glands secrete a mucilaginous substance which is utilized by the insect in the production of the spittle. Mixed thoroughly with the anal secretions it serves to render this viscid and thus to hold the air bubbles blown into it. This view is based upon the following experiments.

The region of the seventh and eighth abdominal segments of several specimens of the nymph was carefully seared by means of a heated needle. These specimens were then placed on a plant and, although badly treated by the operation, soon found suitable places and began to suck up the juices, and as usual became enlarged. In the majority of cases each nymph began to emit drops of fluid from the anal opening. Although during the emission of this fluid the caudal segments of the abdomen were extended and retracted as in the normal specimen, in no case were bubbles formed within the secretion. This was true even after twelve to fourteen hours. In order to test whether this was due to the lack of some constituent normally secreted by the injured glands, air was blown into the fluid through a finely pointed tube; instead of being retained, none of the air balls remained in the fluid more than five to ten seconds. On the other hand, bubbles blown into the secretion of unseared specimens held in it for a very long time. This experiment was repeated many times over and always with the same result.

Other Supposed Sources of the Secretion

Besides these glands, other structures have been mentioned as participating in the formation of the froth, and in order to determine what part they played in it they were given careful consideration.

Berlese (1907) regards the glands of Batelli as the sole source of the secretion. This, my observations, confirming in part those of Morse and others, have shown conclusively to be incorrect. While I hold that the above-mentioned glands contribute an important element to the spittle, there is not the slightest question but that the fluid portion is emitted from the anal opening.

We have seen that Porta (1900) considered the secretion as formed primarily by glands scattered among the hypodermal cells of the abdomen and opening to the surface through prominent canals, and that these were especially abundant in the region of the stigmata. All that could be noticed were the openings of trichopores.

A study of longitudinal and cross sections failed to show any such glands as described and figured by Porta. There are to be found the prominent oenocytes which are more numerous in the ventral surface of the animal. Berlese (1907) dismisses this view by stating that it is these oenocytes which Porta has mistaken for spittle glands. While this is doubtless in part true, I believe, as near as can be judged by the imperfect illustrations, that Porta was also misled by oblique sections through the body wall.

Porta (1900) mentions an oval gland which he says is situated in the fourth somite near the intestine, which he further states is ductless and has no connection whatever with the intestine or any other organ. He thinks that it may be concerned in the formation of the spittle, though he gives no tangible reason in support of this view. After careful study of a number of series of sections I failed to find any such independent gland and I am convinced that he in reality had under observation one of the cephalic glands and that of course it has no relation to the spittle secretion.

This same writer describes other glands which he considers are concerned indirectly in the production of the spittle. These he describes as being situated in the latero-ventral region of the third, fourth, fifth and sixth abdominal segments. He states that there are four pairs of these glandular masses, and in these ramify numerous tracheæ. He was unable to find any external openings to these glands and did not notice their connections with any other organs. The fact is that they are accessory reproductive organs, and that in perfect series their connection with this system may be most readily traced.

SUMMARY

The secretion of the spittle insect is made up from two sources:

The fluid portion is the anal secretion into which the insect by means of caudal appendages introduces numerous air bubbles.

The glands of Batelli secrete a mucilaginous substance which, added to the anal fluid, renders it viscous and thus causes the retention of the air bubbles.

The so-called branchial appendages of Morse and of Porta are merely plates of this mucilaginous secretion.

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